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Concealment in a dynamic world: dappled light and caustics mask movement

Samuel R. Matchette [a, b, *], Innes C. Cuthill [a], Nicholas E. Scott-Samuel [b]

[a] School of Biological Sciences, University of Bristol, Bristol, U.K.
[b] School of Experimental Psychology, University of Bristol, Bristol, U.K.

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The environment plays a significant role in shaping the visibility of signals both to and from an organism. For example, against a static background movement is highly conspicuous, which favours staying still to optimize camouflage. However, backgrounds can also be highly dynamic, such as areas with wind-blown foliage or frequent changes in illumination. We propose that these dynamic features act as visual noise which could serve to mask otherwise conspicuous movement. Two forms of illumination change were simulated, water caustics and dappled light, to represent dynamic aquatic and terrestrial environments, respectively. When asked to capture moving prey items within the simulated scenes, human participants were significantly slower and more error prone when viewing scenes with dynamic illumination. This effect was near identical for both the aquatic and terrestrial environments. In the latter, prey item movement was also found to be masked most often when the pathway taken involved movement across the dynamic dappled areas of the scene. This could allow particularly moving prey to reduce their signal-to-noise ratio by behaviourally favouring the relative safety of environments containing dynamic features.

Many organisms have evolved camouflage to reduce detection and subsequently evade predation (Cott, 1940; Endler, 1981; Ruxton, Sherratt, & Speed, 2004; Stevens & Merilaita, 2009; Thayer, 1909). For traditional camouflage strategies, such as background matching, this involves an organism matching (elements of) the surrounding background while remaining largely stationary (Cuthill et al., 2005; Endler, 1981, 1984; Merilaita & Stevens, 2011; Stevens & Merilaita, 2009). However, many natural backgrounds have dynamic components, not just in the physical movement of plants in wind or underwater currents (New & Peters, 2010; Peters, Hemmi, & Zeil, 2007), but also in their illumination (Endler, 1993; Endler & Théry, 1996). Here we investigated the effect on prey detection of two forms of rapid variation in the illumination: underwater caustics and dappled light through foliage.

As light passes through the spatially heterogeneous surface of water, it is diffracted in a way that diverges then converges the rays to form patterns of variable irradiance upon the substrate: these irradiances are known as water caustic networks (Lock & Andrews, 1992; Swirski, Schechner, Herzberg, & Negahdaripour, 2009). As the water moves naturally, these networks flicker, changing in both space and time (Lock & Andrews, 1992; Swirski et al., 2009). Analogously in terrestrial environments, dappling is a consequence of light passing through foliage that, when naturally swaying with the wind, casts moving shadows onto the substrate. These shadows can be low to very high contrast (with respect to the surrounding, directly illuminated, areas) and, depending on the strength of the wind, can be anything from static to highly dynamic. Both examples of illumination variation are likely to be large sources of natural visual noise, decreasing the signal-to-noise ratio for visually oriented organisms (Merilaita, Scott-Samuel, & Cuthill, 2017), but each has an influence at a different scale. Dynamic water caustics cause changes in illumination across the whole scene (global scale), whereas dappled light has most effect on illumination locally at the margins of shade (local scale) and therefore one would expect issues with detection to be closely associated with these margins.

Visual noise, such as the movement of foliage, can alter behaviour, especially that involving signals. Ord, Peters, Clucas, and Stamps (2007) observed that the speed of vertical head-bobs and dewlap expansion displayed by territorial anole lizards, *Anolis cristatellus* and *Anolis gundlachi*, correlated strongly with the

* Correspondence: S. R. Matchette, Office 2B09, School of Biological Sciences, University of Bristol, Bristol Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, U.K.
E-mail address: sm12340@bristol.ac.uk (S. R. Matchette).

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varying speed of wind-blown background vegetation. Similarly, Peters et al. (2007) reported that the duration of aggressive tail flicks between rival Jacky dragon lizards, *Amphibolurus muricatus*, dramatically increased when the leafy surroundings were subjected to artificially increased wind, versus ambient wind conditions; this response differentiated the tail-flicking signal from the surrounding moving foliage (Peters et al., 2007). As with all signals, there are benefits from maintaining the signal-to-noise ratio, the failure to do so here being a potential loss of territory or resources to a rival (Ord et al., 2007; Peters et al., 2007).

Whereas communication typically requires increasing the signal-to-noise ratio, traditional camouflage strategies require the opposite (Merilaita & Stevens, 2011). Therefore, just as dynamic signals must be distinct from background motion noise, dynamic cues, such as organism movement, will only go undetected if they fall within the distribution of background motion noise: in general, motion 'breaks' camouflage (Cott, 1940; Hailman, 1977; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Rushton, Bradshaw, & Warren, 2007; Stevens, Yule, & Ruxton, 2008; Zylinski, Osorio, & Shohet, 2009). Fleishman (1985) highlighted this phenomenon with the neotropical vine snake, *Oxybelis aeneus*, a stalking predatory species that shows rhythmic pendulous movement that coincides with the motion of wind-blown foliage. Using artificial wind, Fleishman (1985) demonstrated that *O. aeneus* consistently initiated this type of movement in response to visual cues of wind-blown vegetation and, on some occasions, to the tactile presence of wind alone. Not only do *O. aeneus* preferentially move during periods of wind-induced visual noise, but do so in a manner that mimics that noise (Fleishman, 1985, 1986). Indeed, many species use this oscillation or 'swaying' behaviour apparently to accentuate a cryptic or masquerade effect, including stick- and leaf-mimicking insects (Bian, Elgar, & Peters, 2016) and lizards of the *Chamaeleo* genus (Gans, 1967). Moreover, Ryerson (2017) found that three species of colubrid snakes preferentially use oscillating behaviour (a 'head bob') in conjunction with a dorsal pattern to mimic wind-blown grass. Indeed, these behavioural findings mirror those in psychophysics: a camouflaged stimulus is harder to detect when moving among multiple 'distractors', objects that are similar in pattern and shape to the stimulus and move at the same speed (Hall, Baddeley, Scott-Samuel, Shohet, & Cuthill, 2017; Hall et al., 2013).

Unlike the motion of the organism, the effect of dynamic illumination on concealment remains largely anecdotal, with most hypotheses addressing the putative role of dappled light in the evolution of certain camouflage patterns (Kitchener, 1991; Poulton, 1890; Thayer, 1909). Allen, Cuthill, Scott-Samuel, and Baddeley (2010) confirmed earlier comparative studies (Ortolani & Caro, 1996; Ortolani, 1999) showing that complex pelt patterns in felids, such as irregular spots, are highly associated with the closed habitats in which they live, perhaps due to the presence of dappled lighting. Further, Givnish (1990) proposed that leaf mottling in short-statured forest herbs represented a form of background-matching camouflage to hide from dichromatic herbivores on a sunlight-dappled forest floor. To our knowledge, there have been no studies of caustics conducted in relation to perception, camouflage and behaviour, although Merilaita and Stevens (2011) have previously inferred that the undulating dorsoventral contrasting coloration line of dwarf and minke whales, *Balaenoptera bonaerensis*, may be an example of background matching for 'dappled light'. In this context, the dappled light mentioned will most likely be water caustics.

We simulated both examples of dynamic illumination in computer-based experiments to investigate the extent to which they influence human perception of both moving and stationary prey items. In addition to creating fully dynamic, realistic simulations, static examples of both illuminants were used to determine which effects are specific to movement as opposed to pattern.

METHODS

The simulated environments and subsequent experimental task were created and executed in Unreal Engine 4 (Epic Games, https://www.unrealengine.com). All stimuli were viewed at 40–50 cm from a gamma-corrected 15″ ELO Entuitive 1525L LCD touch monitor (Elo Touch Solutions Inc., Milpitas, CA, U.S.A.), with a refresh rate of 75 Hz and a resolution of 1024 × 768 pixels.

Each trial consisted of participants being presented with one prey item within a simulated scene. The task was to search and capture, by touching, the prey item. Participants had 8 s and one opportunity to touch the prey item. There were two experiments, differing only in the simulated environment: experiment 1 used simulated dappled light upon a leaf litter background while experiment 2 used simulated water caustics upon a pebbly sea bed background (Fig. 1). Both backgrounds comprised one single image, sourced from the software's default asset package, which was tiled repeatedly to make up a background scene. We used the selected background scenes 'out of the box', with range and mean of RGB values as supplied by Unreal Engine, as these were already judged to be realistic. The target luminance was then adjusted to match the mean background luminance. The monitor settings, and thus the luminance experienced by participants, was adjusted so that there was no clipping (saturation at the lower or upper end of the luminance range). The scene covered a screen area of 1024 × 568 pixels and had a mean luminance of 88 cd/m^2 (experiment 1) and 97 cd/m^2 (experiment 2). Each scene was monochromatic and was viewed from a bird's eye perspective. Prey items could appear anywhere in one of two regions (384 × 568 pixels) within this scene (Fig. 1). The location constraint was chosen such that the item never left the screen during a moving trial. The prey item was a three-dimensional sphere with a matt surface and mean luminance equal to that of the background. When viewed from above, as in the experiment, the prey item had a circular area of 255 pixels (Fig. 1) but retained apparent depth due to the realistic projection of shadows upon a three-dimensional object. Once they appeared, prey items could either remain stationary or begin to move. Movement was fixed at a speed of 30 mm/s (3.4 degrees/s) and could occur in any direction. Appearance location, within the specified zones described earlier, and movement direction were random, picked from discrete uniform distributions using Unreal Engine's random integer generator. The simulated dappled light and water caustics were either static or dynamic (with the parameters controlling dynamism kept consistent throughout all dynamic trials). The combination of prey item and scene dynamism formed a two-by-two factorial design. Owing to the restricted locality of visual noise in trials with dappled light (the dappling was created from light passing through the leaves of virtual trees, the latter being stationary), four different zones of the environmental scene in experiment 1 were used. Each zone provided a different arrangement of trees and therefore a different arrangement of dappling. Two primary measures were recorded for each trial: outcome (hit, miss or time out) and response time to the nearest 10 ms (for hits and misses). An additional measure for experiment 1 was the pathway for moving prey items in relation to the levels of shade and open light encountered. These pathways were classified with respect to the time in direct light (versus shade) into one of five bins: 0–5%: shade only; 5–45%: mostly shade; 45–55%: shade/light mix; 55–95%: mostly light; 95–100%: light only. For further details of scene and trial generation see the Appendix. Example trial clips are available in the Supplementary Material.

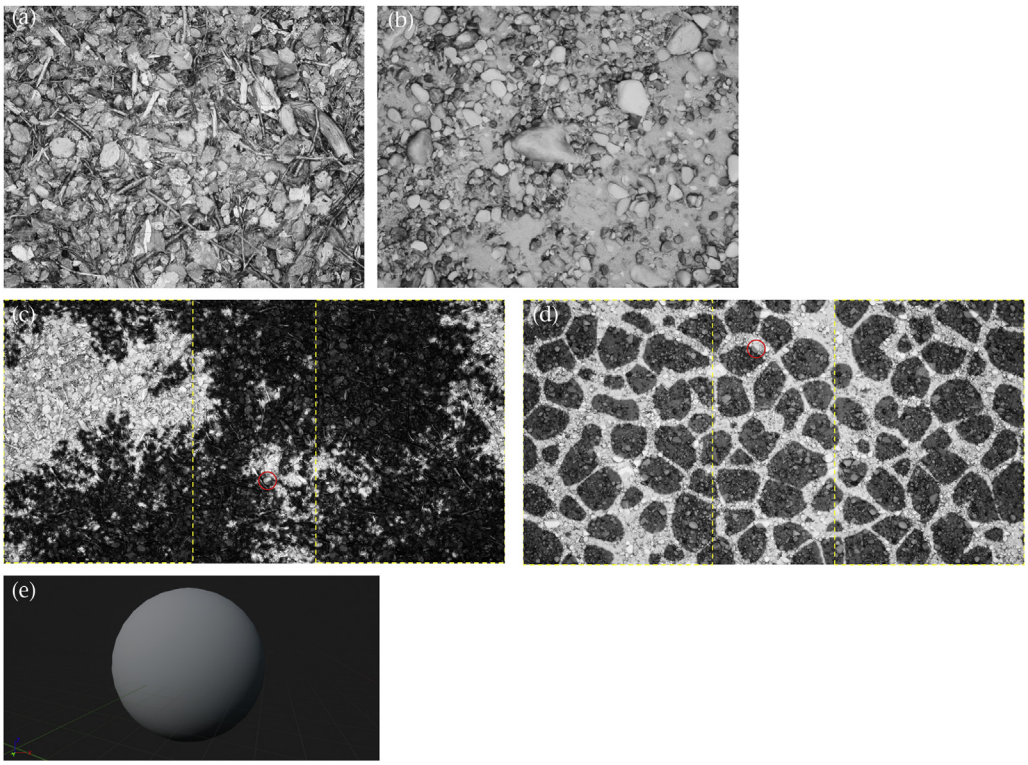

Figure 1. (a, b) Screenshots of the tiled images used as backdrops: (a) leaf litter for experiment 1 and (b) pebbles for experiment 2. (c, d) Screenshots of a trial from treatment 1 in (c) experiment 1 and (d) experiment 2. The two regions denoted by the dashed yellow lines are the possible prey item appearance areas (no lines were present in the actual trials). In both, the prey item (artificially highlighted by a red circle) is mid-way through moving from one appearance area towards the other. (e) A close-up of the prey item outside of the experimental context. Gridlines and edge transparency are artefacts of the Unreal Engine editor window.

A total of 40 participants (37 females and three males, aged 18–22) were recruited opportunistically from the Psychology undergraduate population of the University of Bristol, with half for each experiment: each was naïve, had normal/corrected-to-normal vision and provided written consent in accordance with the Declaration of Helsinki. The experiment was approved by the Ethics of Research Committee of the Faculty of Science, University of Bristol. There were 200 trials per participant (50 replicates of each of the four treatments), in an order independently randomized for each participant. A single practice trial for each participant prior to testing was used to demonstrate the features of the scene and trial, as well as to ensure that participants could correctly identify the prey item. Each trial was separated by a break screen, which was blank but for the trial number and instructions for continuing. The trial number was displayed in either green or red font depending upon whether the participant succeeded or failed to capture the prey item in the previous trial. The scenes chosen contained elements that were similar in size and shape to the prey item (e.g. leaves and pebbles) and therefore we wished to provide feedback on detection success to ensure that participants were attending closely to the task. Touch input was required to continue to the next trial. Each trial was completed in darkness (to remove screen glare) and with headphones on (to remove unnecessary auditory distractions).

All statistical analyses were performed in R (R Foundation for Statistical Computing, www.R-project.org) and utilized linear mixed models and generalized linear mixed models (functions lmer and glmer, respectively, in the lme4 package, Bates et al., 2017). Participant was included as a random effect to account for the repeated measurements from same subjects. The response variables were response time (Gaussian error), proportion of trials with time-outs (Time-outs, binomial error) and proportion of trials when the prey item was missed (Misses, binomial error). For each experiment, the full model included the fixed effects illuminant (static/moving) and prey item (static/moving), plus their interaction, and the random effect of participant. The change in deviance between models with and without the predictors of interest was tested against a chi-square distribution with degrees of freedom equal to the difference in degrees of freedom between the models. If there was insufficient variance present for the full model to converge (e.g. 100% detection success for some conditions), a minimal adequate model was fitted and a likelihood-ratio test (LRT) applied.

RESULTS

In both experiments, there was a significant interaction between motion of the illuminant and motion of the prey item for all response variables (experiment 1: response time: $\chi^2_1 = 17.34$, $P < 0.001$; Fig. 2a; Time-outs: $\chi^2_1 = 47.30$, $P < 0.001$; Fig. 2b; Misses: $\chi^2_1 = 13.20$, $P < 0.001$; Fig. 2c; experiment 2: response time: $\chi^2_1 = 23.95$, $P < 0.001$; Fig. 2d; Time-outs: $\chi^2_1 = 44.33$, $P < 0.001$; Fig. 2e; Misses: $\chi^2_1 = 6.15$, $P = 0.013$; Fig. 2f). To explore the cause of these interactions, stationary and moving prey trials were analysed separately (Table 1). For moving prey, participants spent significantly longer, were timed out more often and missed the prey item more often, when in the presence of dynamic dappled light than when in the presence of static dappled light. With static prey items there was typically either no effect of motion of the illuminant light (response time, both experiments; Time-outs and Misses, experiment 2) or a reduced effect (Time-outs, experiment 1); but for Misses in experiment 1, the effect was greater, although still in the same direction as for moving prey (more misses with moving dappled light).

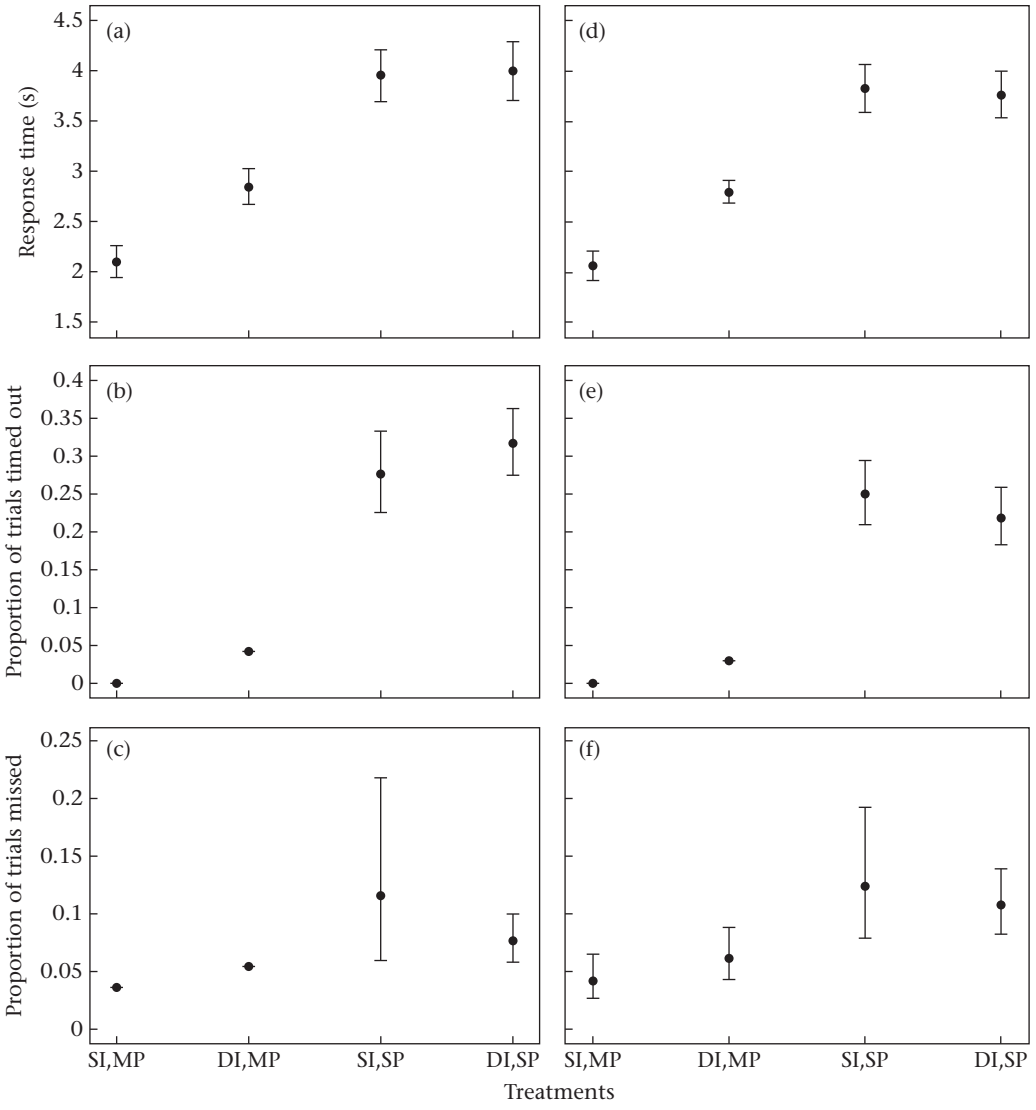

Figure 2. Plot grid for all response variables for (a, b, c) experiment 1 and (d, e, f) experiment 2. Treatment abbreviations: SI (static illuminant), DI (dynamic illuminant), SP (stationary prey) and MP (moving prey). (a, d) Mean response times for the treatments. Error bars indicate 95% confidence intervals derived from the linear mixed models. (b, e) The proportion of trials timed out and (c, f) the proportion of trials missed for each treatment. Error bars indicate 95% confidence intervals derived from generalized linear mixed models. Confidence intervals for the two moving treatments with proportion of time-outs (b, e) could not be estimated because the model for moving items did not converge. This was because there were never any time-outs for moving items and no caustics, and very few for moving and caustics. Without any variance in one treatment, the maximum likelihood could not be estimated with confidence.

Table 1
Effects of motion of the illuminant on prey item detection, when prey were moving or static

	Moving prey		Static prey	
	χ^2_1	*P*	χ^2_1	*P*
Experiment 1 (dappled)				
Response time	35.51	<0.001	0.10	0.763
Time-outs	58.01	<0.001	4.11	0.043
Misses	4.72	0.030	10.78	0.001
Experiment 2 (caustics)				
Response time	50.58	0.001	0.34	0.559
Time-outs	42.00	0.001	2.59	0.107
Misses	4.59	0.032	1.39	0.239

The response variables are response time, proportion of trials with time-outs (Time-outs) and proportion of trials when the prey item was missed (Misses).

Pathway (Experiment 1 Only)

Water caustics, being generated by light passage through waves, have a more regular spatial distribution than the dappled forest light, which is necessarily clustered under leafy branches. Therefore, there was greater variation in the extent to which prey pathways passed through varying illumination in experiment 1 (forest) than in experiment 2 (underwater). We therefore predicted within-treatment differences in experiment 1, with search being more difficult in trials where pathways crossed greater mixtures of shade and light. Fig. 3 shows the response time and the proportion of time-outs plotted against the pathways taken by moving prey items. There was a significant interaction between the presence of dapple and the pathway bin for both response variables with moving prey items (response time: LRT = 38.78, $P < 0.001$; Time-

outs: $\chi^2_1 = 40.93$, $P < 0.001$). The slowest response times were associated with pathways that crossed a larger mix of shade and light pixels ('mostly shade', 'shade/light mix', 'mostly light'). This effect was accentuated when participants viewed the same pathways in the presence of dynamic dappled light instead of static dappled light. The proportion of time-outs too were highest in mixed pixel pathways ('mostly shade', 'shade/light mix', 'mostly light'). The effect of dappled light on the proportion of time-outs was only found to be significant for moving prey items in the presence of dynamic dappled light: no time-outs were recorded for moving prey items in static dappled light.

DISCUSSION

Prey detection was adversely affected in the presence of simulated dynamic dappled light and water caustics. In particular, our results highlight the considerable effect that dynamic illumination has upon the perception of moving prey, an effect that is near-identical for both our terrestrial and aquatic simulations. For moving prey items within dynamic scenes, the response time for finding the item, as well as the number of time-outs and misses associated with the task, were significantly greater than trials with a static scene. This demonstrates how dynamic illumination, as with dynamic visual noise caused by movement of background objects (New & Peters, 2010; Peters et al., 2007), can mask motion signals. Similarly to background complexity (Dimitrova & Merilaita, 2010, 2012; Merilaita, 2003; Xiao & Cuthill, 2016), the signal-to-noise ratio is reduced (Merilaita et al., 2017). Although movement 'breaks' camouflage (Cott, 1940; Hailman, 1977; Hall et al., 2013; Rushton et al., 2007; Stevens et al., 2008; Zylinski et al., 2009), an effect also seen in the slower response times and detection probabilities for static prey in our experiments, movement in an environment with dynamic illumination is safer than one without. The significance of this masking effect, over a timescale that represents a fleeting encounter in nature, may be important for providing prey additional time to (1) flee and reach the safety of a burrow or enclave or (2) prepare secondary antipredator defences, for example startle displays (Cott, 1940; Edmunds, 1974; Umbers, Lehtonen, & Mappes, 2015), thanatosis (Edmunds, 1974; Gallup, 1977; Ratner & Thompson, 1960; Rovee, Kaufman, Collier, & Kent, 1976) or retaliatory behaviour (Edmunds, 1974; Ruxton et al., 2004). Moreover, this masking effect is seemingly consistent not only between simulated aquatic and terrestrial environments, but also across the local and global scales of dynamic illumination influence.

The influence of dynamic illumination is also apparent when we consider its effect upon the pathways and locations of the prey items (Fig. 3). For prey items moving in the presence of dynamic dappled light, we found slower response times and the most recorded time-outs for pathways that involved movement through a mix of light and shaded ('mostly shade', 'shade/light mix', 'mostly light') than purely through shade and light ('shade only', 'light only'). In addition, we found no recorded time-outs for the 'shade only' pathways,

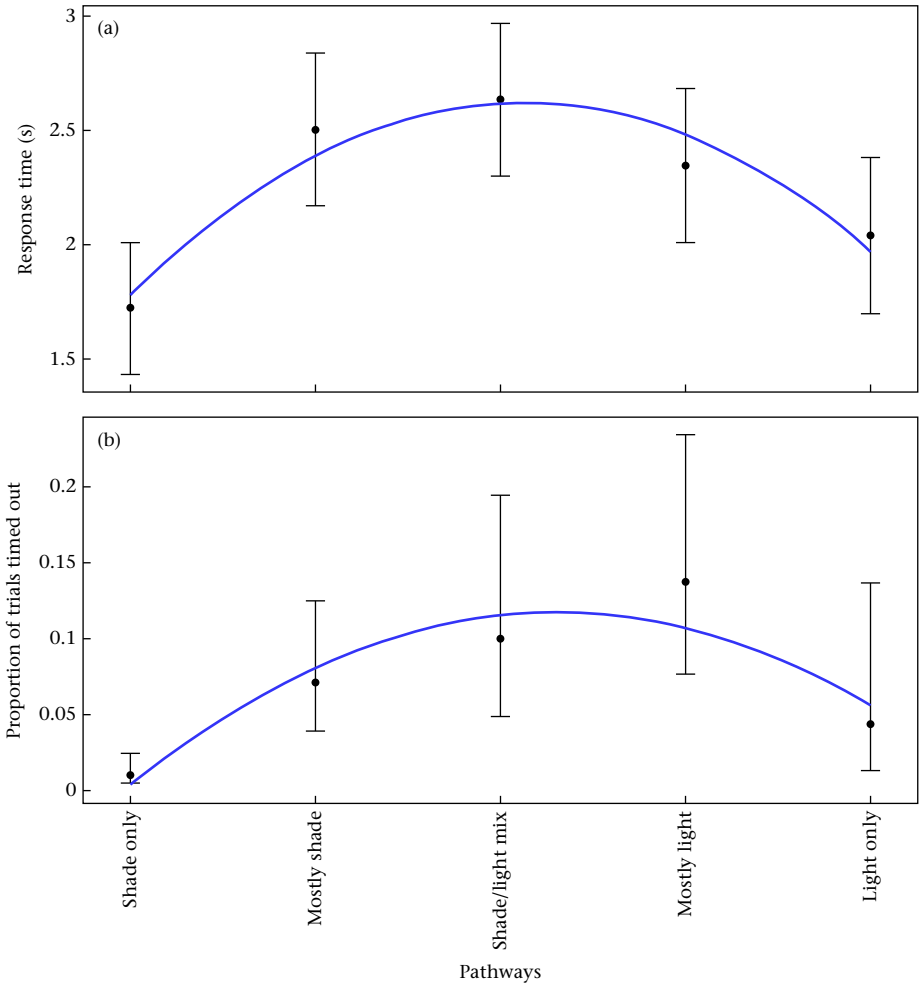

Figure 3. Pathway comparisons for moving prey items in the presence of dynamic dappled light by (a) response time and (b) proportion of time-outs for experiment 1. Error bars indicate 95% confidence intervals derived from linear mixed models (a) and generalized linear mixed models (b). Both data sets are fitted with a quadratic (blue line).

or any recorded time-outs for all pathways in the static dappled light treatment. Indeed, when moving along pathways with minimal visual change, the environment is relatively static and therefore movement is more conspicuous. This demonstrates that, at least for localized dynamic illumination such as dappled light, the presence of dynamism in the wider visual scene is not enough to mask movement but, instead, movement needs to occur across the boundaries of illumination change for it to be disguised.

Remaining stationary maximized concealment in both experiments, with this effect relatively unaffected by the presence of dynamic illumination. This was not a ceiling effect, because more prey were detected within the time limit than not. This suggests that the effect of dynamic lighting is not via a nonspecific increase in visual complexity, but via increased noise in the domain that renders prey most salient: motion.

There were consistently faster response times and fewer time-outs for prey items found in shaded locations in experiment 1. There are two reasons why this may be the case. First, it could be an effect of participants optimizing search efficiency, which, in part, is a consequence of the scene ratio: there was a greater proportion of shade than light in the simulated scenes. Participants, therefore, could optimize their visual search by (1) searching in relatively homogeneous regions (either shade or light) and (2) searching in the most common background first (shade). Second, and not mutually exclusively, participants might have become adapted to a relatively dark background and so their contrast detection might have become impaired when switching to fixate on an entirely light area of the scene. This would additionally explain the slower response times found for 'light only' pathways for moving prey items (versus 'shade only' pathways), but also why they were never as slow as the mixed light pathways. Overall, the difference in detection levels for items in the open light areas of the scene remains interesting, as it defies the expected effect that higher colour contrast has upon conspicuousness in these areas (Théry, 2001).

Overall, our results emphasize the importance of considering the surrounding environment, as well as the target, and suggest a novel way in which camouflage and behavioural strategies can be directly influenced. Care should be taken when generalizing our results, given that the scenes in the experiment were generated using software designed for gaming graphics, not psychophysics. That said, Unreal Engine is a highly successful, multi-award-winning, games platform because the generated scenes are perceived as realistic and immersive. We therefore believe it provides a useful paradigm intermediate in complexity between a typical computer-based laboratory experiment on visual search and a relatively uncontrolled, but ecologically valid, field experiment. Indeed, to limit the complexity of the current study, there were several environmental factors that were standardized but that would be highly variable in nature: the strength of the wind generating the waves and foliage movement, the type and size of foliage, the distance between the water/foliage surface and the surface upon which the light show was projected, as well as the size of prey and the type of movement they demonstrated. All would significantly influence the detectability of prey movement and therefore warrant further investigation.

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Supplementary material

Supplementary material related to this article can be found at https://doi.org/10.1016/j.anbehav.2018.07.003.

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Appendix

Scene Generation: Dappled Light

Seven key components formed the core of each experimental zone: (from bottom up) floor, spawn areas, prey item, magnet item, camera item, tree static mesh collection and the lighting systems. Each had particular settings and 'blueprints' associated with it, which could be coded in various ways to alter performance and behaviour. Multiple experimental zones were used.

The floor component was a standard plane static mesh, coated in a default material acquired from the free demonstration asset package, 'Kite Demo'. The material attached to the floor component ('forest_path_1') was a tiled, high-quality image of leaf litter (Fig. 1). This formed the backdrop to all dappled light trials in this experiment. Set just upon this were two transparent box meshes that would act as 'spawn' (appearance) areas, one for the target (the prey item) and the other for its necessary partner (the magnet item). The prey item was represented by a spherical static mesh and could be manipulated in multiple ways, using the relevant blueprint to change the material, the movement and the interactivity with the player and surrounding game components. The magnet item was represented by a cube static mesh and remained both static and transparent. Both prey item and magnet item spawned at a random location within their respective spawn areas at the start of each trial. A projectile movement component was attached to the prey item that, when activated, would cause the prey item to home (at any desired speed) towards the magnet item, allowing countless random movement vectors to be created as desired. The spawning areas (Fig. 1) were sized so that the nonspawning region between the two was of an appropriate size. At the desired speed, even if prey items and magnet items spawned at the shortest possible vector, the prey item would not quite reach the magnet item in the 8 s time limit. If this region had been smaller, there would have been a risk that at the shortest possible vector the prey item could reach and hit the magnet, subsequently stopping, with time in the trial to spare. This would confuse the dichotomy between moving and stationary prey items.

Above this ground activity, a camera item was positioned, which would provide the player view for each trial. The camera item was rotated 90 degrees to the floor component and had equalized RGB values, creating a monochrome bird's eye view of the leaf litter backdrop. Between this component and the lighting systems were a collection of randomly positioned, pre-made model tree static meshes, also of the 'Kite Demo' assets package. When paired with the lighting systems described above, these cast the characteristic dappled light shadows across the floor component. Each experimental zone had a unique arrangement of trees and therefore a unique arrangement of shadows. Crucially, a highly editable noise component could be added to create a range of dappled light flickers and dynamic shadows, to mimic the changing strength of wind. High above each zone was a directional light source and a skylight. Each had an intensity scale which would alter both the light intensity (brightness) and the shadow intensity (darkness).

Scene Generation and Structure: Caustics

The graphical generation of the caustics environment mimicked the format and set-up of the dappled light environment in all but two ways. First, the leaf litter material attached to the floor component was replaced with that of a pebbly river or sea bed. This image ('pebbly_river') was included within the 'Kite Demo' asset package (Fig. 1). Second, the tree static meshes used to create the dynamic shadows were replaced with a plane static mesh. The material for this static mesh was composed of particular images held in a material array. These images were created using the free 'Caustics Generator' (Dual Heights, https://www.dualheights.se/caustics/) which provides a set of frames for a small animation of simulated caustics. Each image was then edited in GIMP2 (GIMP, https://www.gimp.org/): it was converted to monochrome, then the black–white contrast was increased and white pixels were converted to the alpha (transparency) channel. Overall, this created an image that was transparent in only the regions that correspond to the caustic network. The material array containing these images was then applied to the water plane. The images, and therefore the plane material, were then changed at very high frequency (every 0.05 s) with the next image in the array order. With enough images in the material array, and over the course of the trial, the resultant lighting effect was a caustic flicker passing through the changing transparent regions of the plane material. Equally, if static caustics were required, the material used for the plane component was simply the first image in the material array.

Post Hoc Measures

For experiment 1, it was necessary to ascertain the pathway or location used by the prey item in each of the four experimental zones. This could only be achieved post hoc. Screenshots of all experimental zones were captured and resized to the resolution of the trials with Microsoft Paint (Microsoft Paint, https://www.microsoft.com/en-gb/). Using GIMP2 (GIMP, https://www.gimp.org/), these screenshots were saturated by luminosity and increased in contrast to create binary black and white images. With a script in Matlab (The Mathworks Inc., Natick, MA, U.S.A.), the images were called in turn for the particular trial and zone used, as well as the starting XY and ending XY coordinates of prey items. Matlab then created a temporary vector, which it searched along for white pixels: the output for this search was the percentage of white pixels encountered and was recorded as such when fed back into the data table.